

THE GENERA OF CISTACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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CISTACEAE Jussieu, Gen. Pl. 294. 1789, "Cisti," nom. cons.

(ROCKROSE FAMILY)

Shrubs, subshrubs, or herbs, often pubescent. Leaves alternate [or typically opposite], simple, entire, pinnately [or palmately] nerved, or sometimes 1-nerved, usually relatively small and narrow, usually bifacial, stipules present or absent. Flowers bisexual, regular, hypogynous, solitary or in cymose (pleio- or monochasial) terminal or axillary inflorescences. Sepals 5 (the outer 2 often bractlike, conspicuously narrower than the inner) or 3, distinct, convolute in bud. Petals 5, rarely 3, or absent (cleistogamous flowers), convolute (in the opposite direction to that of the sepals) in bud, rarely imbricate, usually ephemeral, very rarely persistent. Stamens numerous, rarely 3–10; filaments distinct, sometimes sensitive; anthers basifixed, 2-locular at anthesis, longitudinally dehiscent; pollen usually 3-colpate, suboblate to prolate, medium sized to large, of various patterns, often reticulate. Gynoecium of 3 [5–10] united carpels; style simple, long to very short or wanting; stigma 1, either large and capitate or discoid (often 3 [5–10]-lobed) or minute, or stigmas rarely 3, fimbriate-plumose; ovary 1- or imperfectly 3 [5–10]-locular, placentae parietal, filiform or shieldlike, often intruded; ovules 2 to many on each placenta, funiculate, orthotropous [rarely anatropous], with 2 integuments and a thick nucellus. Capsule loculicidal, 3 [5–10]-valved, 3- to many-seeded. Seeds usually small, with starchy, often hard endosperm (nuclear in development); embryo curved in the form of a hook or ring, or \pm circinate [or plicate to biplicate], rarely almost straight; seed coat of 2 integuments,

¹ Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296–346. 1958) and continued through those in volumes 40–45 (1959–1964). The area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

The author is indebted to Carroll E. Wood, Jr., for his criticism and many valuable suggestions, and to Mrs. Gordon W. Dillon, for her careful help in the preparation of the manuscript.

the outer thin, delicate, membranaceous, often gelatinous when moist, sometimes collapsed and deformed, the inner hard. TYPE GENUS: *Cistus* L.

A family of seven genera and about 200 species, primarily of the warm-temperate regions of western Eurasia, North Africa, North America, and South America (a few species of *Helianthemum* subg. *Lecheoides* in Chile, southern Brazil, Uruguay, and Argentina), with the strongest concentration of species in the Mediterranean region, especially the Iberian Peninsula. There are notable extensions northward into the subarctic (*Helianthemum nummularium*, in Karelia in Europe; *Hudsonia tomentosa* Nutt., in northern Alberta and probably in southern Mackenzie in North America) and southward into the tropics (a few *Helianthemum* species in the western Sahara, one in the mountains of central Costa Rica, and two in Hispaniola). In North America the family is represented by *Hudsonia*, *Lechea*, and subg. *Lecheoides* of *Helianthemum* and is centered in the Atlantic Coastal Plain.

Cistaceae, in general, are chamaephytes inhabiting dry, sunny sites in lowlands to mountains (rarely at high altitudes) and often showing a preference for sandy soils. Reproduction by fragmentation of underground stolons has been recorded in some Old World species of *Cistus* and *Helianthemum* (Gaume).

An ecto- and endotrophic mycorrhizal association has been found in *Helianthemum nummularium* (Boursnell). The fungus, which spreads through the plant and infects the outer "gelatinous" coat of the seeds, is necessary for germination, apparently supplying the developing seedling with thiamin, without which the young plant will not grow. A fungus in the seed coat and roots is probably found throughout the Cistaceae, as is suggested indirectly by the absence of root hairs in all seedlings of 15 species of *Helianthemum*, *Cistus*, *Tuberaria*, and *Fumana* which Gaume investigated.

Apparently there are no adaptations for seed dispersal, although it has been suggested that the gelatinization of the outer seed coat in moist weather could favor dispersal by small animals. Usually the seeds falling from the capsules seem to remain close to the parent plant. Germination is epigeal. Starch grains have been found in the epidermis of the outer seed coat in several genera.

Glandular (uniseriate and sometimes capitate) and nonglandular (simple, "falsely bicellular," tufted, stellate and rarely peltate) hairs are useful in at least some cases in distinguishing the species. The simple, "falsely bicellular" hairs, which appear (when mature) to have a second hair included in their basal portion, have been recorded only in Cistaceae (*Lechea*, to some extent in *Hudsonia*, and sporadically in other genera) and in Combretaceae.

The flowers usually open in sunshine, sometimes for only a few hours. They are visited for pollen by a variety of hymenopterous, dipterous, and coleopterous insects. Complete self-sterility has been observed in *Cistus*, and some European species of *Helianthemum* seem to be more or less self-

incompatible. In most other genera cross-pollination and self-pollination have been reported, the latter occurring in the case of failure of insect pollination. Cleistogamy is widely distributed, occurring either occasionally in normally chasmogamous species (e.g., some species of *Cistus*, *Tuberaria*, and the European and American subgenera of *Helianthemum*) or, as a rule, in several species of *Fumana* and *Helianthemum* sect. *Eriocarpum* and in most of the species of sect. *Lecheoides*. Polyembryony has been recorded in *Cistus hirsutus* Lam. and *Helianthemum grandiflorum* Kerner.

Numerous natural and artificial interspecific hybrids in *Cistus*, *Halimium*, and *Helianthemum* sect. *Helianthemum* are known, and hybrids in *Lechea* seem probable. A hybrid origin for *Hudsonia tomentosa* var. *intermedia* Peck has been suggested (Hall). About 15 more or less fertile natural intergeneric hybrids (\times *Halimiocistus*) between species of *Cistus* sects. *Halimioides* and *Halimium* are known. Chromosome counts, including only one on an American species, cover about 20% of the family and a very limited part of the ranges of the species. The family appears to be aneuploid (*Cistus*, $2n = 18$; *Halimium*, $2n = 18$; *Helianthemum*, $2n = (10), 20, 22$; *Tuberaria*, $2n = 14, 24, 36, 48$; *Fumana*, $2n = 32$). All the counts in *Cistus*, the most primitive genus, suggest nine as the basic chromosome number of the family. On this basis, polyploidy (at present evident only in *Tuberaria* and *Fumana*) seems to be rare but probably played a part in the origin of some species and genera. Chromosome numbers, as well as pollen morphology (Heydacker), appear to support the existing classification of the genera and sometimes of subgenera of Cistaceae.

Cistaceae are most closely related to Bixaceae, but a relationship with Violaceae through Flacourtiaceae seems very probable. An affinity to Capparales, especially Resedaceae and Capparaceae, has also been suggested. A close relationship between Cistaceae and Hypericaceae has been disproved and the considerable similarities of these families explained by parallel evolution (cf. Vestal).

Economically the family is of slight significance. Two Mediterranean species of *Cistus* yield ladanum or labdanum, a fragrant oleoresin used in incense and perfumery. The young shoots of *Helianthemum canadense* contain about 10% tannic acid and a *Helianthemum*-glucoside. The species is said to be used as a remedy against scrofulae, and the local use of shoots of *Lechea villosa* (*L. mucronata*) as a tonic and febrifuge has been recorded. Several species of *Cistus*, *Halimium*, and *Helianthemum* are grown as ornamentals.

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KEY TO THE GENERA OF CISTACEAE

- A. Petals 5, convolute in bud, yellow, fugacious, or wanting; stigma 1; ovary and capsule 1-locular with filiform placentae.
 - B. Leaves with flat or merely revolute blade, flowers (our spp.) of two kinds, the earlier chasmogamous with broad petals, the later cleistogamous with petals reduced or more often wanting; style short or wanting, stigma large, usually capitate, often \pm 3-lobed; embryo curved in the form of a hook or ring to \pm circinate; erect subshrubs or perennial herbs. 1. *Helianthemum*.
 - B. Leaves scalelike or subulate; flowers uniform, with relatively narrow petals; style elongate, slender, stigma minute; embryo coiled into the form of a closed hook; bushy, heathlike, low subshrubs. 2. *Hudsonia*.
- A. Petals 3, imbricate in bud, reddish, marcescent; stigmas 3, fimbriate-plumose, red, sessile or subsessile; ovary and capsule incompletely 3-locular with broad, shieldlike placentae; embryo nearly straight to curved; low suffruticose or herbaceous flaxlike perennials, mostly with overwintering basal leafy shoots. 3. *Lechea*.

1. *Helianthemum* Miller, *Gard. Dict. Abr. ed.* 4. 1754.

Herbs or subshrubs [or shrubs], usually pubescent with stellate hairs; leaves alternate [or opposite], flat, sometimes slightly revolute, pinnately veined, relatively small and narrow, 1–3.5(–5) cm. long, linear, oblong to oblanceolate, rarely obovate, usually short-petioled or subsessile, exstipulate [or stipulate]. Flowers dimorphic [or homomorphic], the earlier chasmogamous, petaliferous, often showy, the later cleistogamous, usually apetalous, sometimes cryptopetalous, pediceled to subsessile, solitary or in few- to many-flowered cymose, raceme-, corymb-, or headlike, sometimes paniculate inflorescences. Sepals 5, the 2 outer bractlike, considerably narrower, shorter to longer than the 3 inner. Petals 5, usually yellow, delicate, fugacious, longer than the sepals, or very small or wanting (in cleistogamous flowers). Stamens numerous, 12–35[–100], with long filaments, or (in cleistogamous flowers) 3–10, with short filaments. Gynoecium 3-carpellate; stigma large, usually capitate, sometimes deeply 3-lobed; style single, terminal, short [long] or wanting; ovary 1-locular, with 3 parietal filiform placentae and numerous (usually 20–80) or, in cleistogamous flowers, relatively few (mostly 3–20) orthotropous ovules on long, filiform funiculi. Capsule 3-valved, few to many seeded, seeds small, smooth, papillose, or reticulate, embryo curved in the form of a hook or ring to \pm circinate [or plicate to biplicate]. (Including *Halimium* (Dunal) Willk. §§ *Spartioides* Grosser and *Lecheoides* Dunal and *Crocantthemum* Spach sensu Britton, Janchen et auct.) LECTOTYPE SPECIES: *Cistus nummularius* L. = *H. nummularium* (L.) Mill. (*H. Chamaecistus*

Mill.); see Rehder, *Bibliogr. Cult. Trees Shrubs* 471. 1949. Name from Greek, *helios*, sun, and *antheon*, flower.) — SUNROSE, FROSTWEED.²

A genus of about 110 species in three subgenera, the range nearly that of the family. Subgenera HELIANTHEMUM (subg. *Ortholobum* Willk.) and PLECTOLOBUM Willk., with about 80 species, are restricted to the Old World. Subgenus LECHEOIDES (Dunal) Reichenb. (LECTOTYPE SPECIES: *H. corymbosum* Michx.) is exclusively American, with about 30 species in two sections: sect. LECHEOIDES, plants usually with dimorphic flowers, occurring in eastern North America and South America with extensions to the West Indies and to Mexico, Central America, and Chile (*H. hirsutissimum* Presl) and sect. SPARTIOIDES (Grosser) Brizicky,³ broomlike subshrubs with homomorphic flowers, known from western North America (California and Mexico), and Chile (*H. spartioides* Presl). About nine species occur in our area. *Helianthemum Nashii* Britton and *H. thyrsoides* Barnh. are restricted to peninsular Florida, while *H. arenicola* Chapm. inhabits coastal sand dunes from northwestern Florida and Mississippi. *Helianthemum carolinianum* (Walt.) Michx., *H. georgianum* Chapm., *H. rosmarinifolium* Pursh, and *H. corymbosum* Michx. are typical Coastal Plain species ranging from Florida northward to North Carolina and westward to eastern Texas and Arkansas, or northward to Virginia and westward to Mississippi (*H. corymbosum*). The two northernmost species, *H. canadense* (L.) Michx., $2n = 20$, and *H. Bicknellii* Fern., centered in the northeastern United States, but the latter reaching 53° latitude in Manitoba, extend southward to South Carolina, northernmost Georgia, and Tennessee, and the latter apparently occurs also in Arkansas.

The American species of *Helianthemum*, which differ from the Old World ones mainly in the alternate leaves, short or wanting styles, and a ring- or hooklike, curved to \pm circinate (*vs.* plicate or biplicate) embryo, have been segregated by some taxonomists from *Helianthemum* (as well as from *Halimium*) as *Crocantemum* Spach (Britton, Janchen, *et al.*) or *Heteromeris* Spach (Ponzo). The difference in the phyllotaxy is hardly essential, for in the American species the lowermost leaves sometimes are opposite and in the Old World species the uppermost alternate. Although in most species of the Old World subgenera the styles are elongated, rather

² The common name sunrose is applicable to the species of *Helianthemum* in general. Frostweed, now employed for designation of all the Atlantic American species of the genus, was originally applied to *H. canadense* because in this species the production of acicular ice crystals from the dead and cracked bark at the root in late autumn was first noticed. Frostwort, adopted in *Standardized Plant Names* (ed. 2, 1942, p. 144) as a common name for all the species of *Crocantemum* (*Helianthemum* subg. *Lecheoides*) has apparently not met with general recognition. The name rushrose has been adopted for the Pacific American species. Rockrose, although often referred to the species of *Helianthemum*, was applied originally and primarily to the genus *Cistus*.

³ *Helianthemum* subg. *Lecheoides* sect. *Spartioides* (Grosser), comb. nov. *Halimium* sect. *Spartioides* Grosser, *Pflanzenreich* IV. 193 (Heft 14): 33. 1903; *Crocantemum* sect. *Spartioides* (Grosser) Janchen, *Nat. Pflanzenfam.* ed. 2. 21: 305. 1925. LECTOTYPE SPECIES: *H. spartioides* Presl.

than short or wanting as in ours, the generic significance of this character seems questionable. Likewise, the distinction in the shape of the embryo does not appear to be absolute. Lubbock (pp. 188, 189) says of some European species, "The embryo of *Helianthemum*, according to Bentham and Hooker, is uncinata, biplicate, or circumflexed. Those coming under my notice are spirally coiled much in the same way as in *Cistus* . . ." Therefore, following Fernald (1917, 1941), the American species are treated here as belonging to a subgenus under *Helianthemum*. The single chromosome count reported for this subgenus, $2n = 20$, a number common in the Old World subgenera, seems to support this view. Palynological evidence also seems to favor the concept of the genus adopted here. Heydacker, who investigated pollen in 55 species in seven genera of Cistaceae (the number of species in each genus unfortunately not given) came to the conclusion that on the basis of pollen characters it would be preferable to retain certain American species, e.g., *H. canadense*, *H. corymbosum*, and *H. scoparium* Nutt. in *Helianthemum*, but in a special section ("tribu"). This conclusion apparently is extendable (on the basis of their close relationships) to all American species of *Helianthemum*, except *H. carolinianum* and *H. brasiliense* (Lam.) Pers., the well-individualized pollen of which supports (according to Heydacker) the retention of the genus *Crocantemum* (apparently in its original delimitation as to include only these two species). However, since at present no other data which might justify the segregation of *H. carolinianum* and *H. brasiliense* are known, both are retained in *Helianthemum* subg. LECH-
EOIDES.

The dimorphism of the flowers is a distinguishing feature of members of sect. LECHEOIDES. The cleistogamous flowers, usually smaller than the chasmogamous, are apetalous or rarely with much-reduced petals and have a lower number of stamens and ovules. They appear either almost contemporaneously and in the same cluster with the chasmogamous or only in autumn and arranged in various inflorescences (the petaliferous then vernal and mostly solitary). No hybrids have been recorded in the subgenus.

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2. *Hudsonia* Linnaeus, Mant. Pl. 11. 1767.

Low, heathlike subshrubs with tufted, diffusely branched stems. Leaves alternate, sessile, small, isolateral, linear-subulate and ascending to spreading or scalelike and appressed and imbricated, softly pubescent, exstipulate. Flowers small, but showy, pediceled or subsessile, solitary at the end of short, leafy branchlets. Sepals usually 3, not quite alike, 1 entire, the 2 others unequally bifurcate at apex or with a tooth or a linear-subulate lobe on the margin. Petals 5, yellow, rarely whitish, obovate-oblong, considerably longer than the sepals. Stamens (8)10–30, filaments filiform, anthers small, ovate or oval in outline. Style elongate, slender, with a minute stigma; ovary 1-locular with 3 navelike placentae, each bearing 2 orthotropous funiculate ovules. Capsule ovoid or ellipsoidal, few seeded, 3-valved, included in the persistent calyx. Seeds ellipsoidal, minutely warty on the surface; embryo coiled into the form of a closed hook. LECTOTYPE SPECIES: *H. ericoides* L.; see Britton & Brown, *Illus. Fl. No. U. S.* ed. 2. 2: 541. 1913. (Named in honor of William Hudson, 1730–1793,

apothecary and botanist, author of *Flora Anglica*, 1762.) — BEACH HEATHER, FALSE HEATHER.

A North American genus of three species ranging along the Atlantic coast from North Carolina to southern Labrador and Newfoundland, inland across Quebec to northern Alberta and probably southern Mackenzie, south- and eastward to North Dakota, Minnesota, Wisconsin, northern Indiana, northern Illinois, Michigan, and northeastern New York. The northernmost, the temperate-subarctic *H. tomentosa*, woolly beach heather, growing on sand dunes along the coast, shores of rivers and lakes, and on sand hills and sandy prairies and pinelands throughout most of the range of the genus, is known in our area only from the seacoast of North Carolina. The occurrence in our area of the northeastern *H. ericoides* L., golden heather, a species primarily of sandy acid pinelands and acidic rocks, seems questionable, and reports from North Carolina need verification. *Hudsonia montana* Nutt., closely related to and perhaps not specifically distinct from *H. ericoides*, is known only from the stony summit of Table Rock (and adjacent peaks in the Blue Ridge, according to Small), in Burke County, North Carolina.

Hybrids between *Hudsonia tomentosa* var. *tomentosa* and *H. ericoides* where these ecologically different species occur together (e.g., along open, sandy highway shoulders running between coastal dunes and pinelands) have been reported by Hall, who considered *H. tomentosa* var. *intermedia* Peck (*H.* × *intermedia* (Peck) Erskine) to be a putative hybrid between the two, since it shows recombinations of characters from both. "The origin of var. *intermedia* is probably not a recent development, i.e., since man built his coastal highways; but more likely in post-Pleistocene, as a result of glacial disturbances of the landscape, opportunity probably existed for these species to hybridize and for the new ecotype to become established."

The genus is quite distinctive in its bushy, heathlike habit, small isolar leaves, prevailing simple, woolly hairs, and three sepals. The basic number of sepals is five, but each of the two outer is completely or partially fused along its margin with the adjacent inner sepal, being apparent as a tooth or a linear-subulate lobe of the latter. Very rarely at least one of the outer sepals is almost distinct. A similar origin for the three sepals of some species of *Halimium* and *Cistus* has been reported by Saunders.

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- Under family references see HEYDACKER, JANCHEN (p. 312), REICHE (p. 306), ROCHE (pp. 81-83), and VESTAL (p. 224).
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3. *Lechea* Kalm ex Linnaeus, Sp. Pl. 1: 90. 1753; Gen. Pl. ed. 5. 40. 1754.

Subshrubs or perennial herbs [frequently biennial in the northern part of the range], subprocumbent to erect, usually strongly branched, mostly with overwintering basal leafy shoots. Leaves generally alternate (the lower cauline and those of the basal shoots sometimes subopposite, opposite, or verticillate), small, ovate to linear or subulate, bifacial, 1-nerved, exstipulate. Flowers minute, 2–2.5 [–4] mm. broad, pyriform to subglobose, short-pedicelated to sessile, numerous, in leafy panicles or in raceme-like inflorescences. Sepals 5, the 2 outer linear-lanceolate to subulate, shorter to longer than the 3 ovate to obovate inner sepals. Petals 3, dark red or reddish, mostly shorter than the sepals, flat and imbricated in bud, marcescent, rarely seen expanded. Stamens 3–25, usually 5–15, filaments filiform, anthers minute, broadly ovate. Stigmas 3, fimbriate-plumose, dark red, sessile or subsessile, ovary short-stipitate, incompletely 3-locular, with 3 shieldlike placentae on incomplete partitions, each placenta usually bearing 2 erect, subsessile ovules, 1 on each side of its posterior face. Capsule narrowly ovoid or obovoid to depressed-globose, incompletely 3-locular or 1-locular, 3-valved, 1–6-seeded. Seeds small, of different shapes, usually 2- or 3-sided, equi- or inequilateral, shining or dull, smooth or reticulate; endosperm hard, sometimes almost transparent; embryo slender, nearly straight to considerably curved. LECTOTYPE SPECIES: *L. minor* L.; see Britton, Bull. Torrey Bot. Club 21: 244. 1894. (Named for Johan Leche, 1704–1764, Swedish botanist and professor of medicine in Åbo.) — PINWEED.

A genus of 17 species centered in eastern North America but extending northwestward to Saskatchewan (*Lechea intermedia* Leggett var. *depauperata* Hodgk.) and southward to Cuba (*L. cubensis* Leggett) and Guatemala (*L. tripetala* (Moç. & Sessé ex Dunal) Britton). Ten species occur in the southeastern United States: *L. cernua* Small, *L. Deckertii* Small (*L. myriophylla* Small), *L. divaricata* Shuttlew. ex Britton, *L. Leggettii* Britt. & Hollick var. *ramosissima* Hodgk., *L. minor*, *L. patula* Leggett (*L. exasperata* Small, *L. prismatica* Small), *L. racemulosa* Michx., *L. tenuifolia* Michx., *L. Torreyi* Leggett ex Britton, and *L. villosa* Ell. (*L. mucronata* Raf.). *Lechea maritima* Leggett, although reported by Small (Man. SE. Fl. 883. 1933) from our area, apparently does not occur south of Virginia.

Although the species are well defined, the specific distinctions are based on rather small technical characters. The basal overwintering shoots (lacking in *Lechea Deckertii*) which appear late in the season and bear crowded, sometimes opposite leaves (usually broader and shorter than the cauline), the calyces (especially the comparative length of the outer and inner sepals), and the fruits and seeds offer the most reliable taxonomic characters.

The species are, in general, inhabitants of dry, sandy, or gravelly,

more rarely rocky, soils near the coast and/or inland on riverbanks, in open woods, fields, barrens, open roadsides, etc. The ecology has not been studied in detail. Distributional patterns are varied. Thus, *L. villosa*, the most widely distributed species, occurs throughout most of eastern North America, south to Florida, west to Texas and northeastern Mexico, Oklahoma, and Nebraska; *L. cernua*, *L. divaricata*, and *L. Deckertii* are endemic to Florida (the last also in southern Georgia); *L. patula* is restricted to the southeastern Coastal Plain; and *L. Leggettii* var. *ramosissima* and *L. Torreyi*, both of the southeastern Coastal Plain, have noteworthy disjunctions in central Tennessee and in British Honduras, respectively.

The flowers, which appear in mid- or late summer, are reported as rarely expanded, except in early morning in bright sunshine. No reliable data are available regarding pollination and fertilization. Kearney stated that *Lechea maritima* may be "safely referred to" as a self-fertilized species, but Hodgdon thought that it "must certainly be to a considerable extent cross-fertilized," since he observed in the field or in herbaria probable, sometimes obvious, hybrids between this species and *L. intermedia*, *L. Leggettii*, *L. minor*, and *L. villosa*. Putative natural hybrids between *L. racemulosa* and *L. villosa* were also recorded by Wilbur and Daoud.

This genus is perhaps the most distinctive of the Cistaceae because of the minute flowers with three imbricated petals, three essentially sessile plumose stigmas and broad shieldlike placentae, the occurrence of basal shoots, the covering of exclusively simple, falsely bicellular hairs, and the small, nearly globular pollen with a distinctive aperture structure.

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